THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SEVENTH SERIES.]

No. 77. MAY 1904.

XXXIX.—*The Phylogeny of the Teleostomi.*

By C. Tate Regan, B.A.

[Plate VII.]

In the following paper I have tried to give an account of the phylogeny of the main groups of the Teleostomi, based on the evidence of the available morphological data. In forming my conclusions I have been helped by criticism and advice from Mr. Boulenger and Dr. W. G. Ridewood, to both of whom I gratefully express my acknowledgments. I trust that the reasons given for differing from the classifications hitherto proposed will prove sufficient: the aim of this paper is constructive rather than destructive, and I have not thought it necessary in every case to give all the available arguments against theories of relationship which I do not accept, but have rather tried to establish the ideas of phylogeny which are here put forward on a sound morphological basis.

The class Pisces, as usually understood, comprises Vertebrates with jaws, with gills supported by visceral arches, and with paired limbs in which the endoskeletal supports have not yet attained the pentadactyle arrangement of higher Vertebrates. Two subclasses may be recognized—Chondropterygii and Teleostomi. The latter are distinguished by the

development of membrane-bones, including an operculum * covering the chamber into which the gill-clefts open.

The Teleostomi may be divided into five orders, the relations of which are expressed in the following diagram :—

The Chondrostei and Crossopterygii correspond to the groups usually so named ; the Dipneusti comprise the Sirenoidei only ; the Placodermi include the Arthrodira, Antiarcha, and Osteostraci ; and to the Teleostei the Ganoidei Holostei are added.

These orders may be defined as follows :—

Order 1. Chondrostei.

Median fins with the dermal rays in greater number than their endoskeletal supports, which are typically in two principal series, baseosts and axonosts, with an outer series of small marginal cartilages. Caudal typically completely heterocercal (rarely abbreviate heterocercal or diphycercal). Paired fins not notably lobate. Pectoral baseosts articulating with an anterior coraco-scapular cartilage and a posterior metapterygium †. Ventrals with a well-developed series of baseosts articulating internally with a series of axonosts, which may be separate or more or less completely fused. Hyostylic. Hyomandibular without posterior process for

* In some specialized forms (*e. g.* Aspredinidæ) the operculum is wanting.

† It is impossible to say whether in the most primitive Teleostomi the metapterygium was already developed or whether it was represented by a series of separate axonosts.

the articulation of the operculum; symplectic not ossified. Branchiostegals not attached to epihyal and ceratohyal. Gular plates, if present, not specially enlarged. Clavicle distinct from the cleithrum. Notochord persistent. Pericardium * communicating with the cœlom.

Order 2. Crossopterygii.

Median fins with the dermal rays often in greater number than their endoskeletal supports, which are often in two series. Caudal heterocercal or diphycercal. Pectorals lobate, with metapterygium often segmented. Ventrals lobate or not, with supports variously arranged. Hyostylic. Branchiostegals replaced by a pair of large gular plates. Clavicle distinct from the cleithrum. Vertebral column variously developed.

Order 3. Dipneusti.

Median fins with the dermal rays in greater number than their endoskeletal supports, which are in two series. Caudal heterocercal or diphycercal. Paired fins acutely lobate, with endoskeletal supports arranged as a segmented axis with or without lateral branches. Autostylic, the palato-quadrate being fused with the cranium and the hyomandibular reduced or absent. Sometimes a pair of large gular plates, but branchiostegal rays never present. Clavicle not distinct from the cleithrum. Notochord persistent.

Order 4. Placodermi.

Median fins membranous, without dermal rays, consisting of a single dorsal, supported by regular series of baseosts and axonosts, and a heterocercal caudal. Pectoral fin, if functional, represented by a jointed Arthropod-like limb, with internal muscles and external dermal plates, sometimes reduced to a fixed spine, or absent. Ventral fin, if present, with a series of baseosts and a single large axonostal cartilage. ?Autostylic. Notochord persistent. Usually a well-developed dermal armour.

Order 5. Teleostei.

Median fins with the dermal rays equal in number to their endoskeletal supports, which are typically in one series, the

* I have taken this character from Bashford Dean, 'Fishes Living and Fossil,' p. 260.

baseosts being either small or absent. Caudal abbreviate heterocercal, homocercal, or diphycercal. Paired fins usually not lobate. Pectoral metapterygium sometimes well developed and serving for the articulation of the posterior baseosts, more often reduced and apparently forming the first of the baseost series. Ventral with the dermal rays directly attached to a single basal bone, the baseosts rudimentary or absent. Hyostylic. Hyomandibular with a posterior process for the articulation of the operculum; symplectic ossified and usually suturally united to the quadrate. Branchiostegal rays attached to the epihyal and ceratohyal. No paired gular plates. Clavicle not distinct from the cleithrum. Vertebral column variously developed. No communication between pericardium and cœlom.

It need hardly be pointed out here that I cannot expect the characters used in the above ordinal definitions to prove constant in every case. Experience shows that, however well defined groups may seem to be, as our knowledge of them becomes more complete annectent forms come to light, and it is self-evident that if we were acquainted with all the forms which have existed we should have a perfect phylogenetic arrangement, but no division into groups. Consequently the generalizations which I have made may or may not be applicable to those unsatisfactorily known extinct forms (*e. g.* Catopteridæ) which can only be provisionally assigned to a position in the system.

Chondrostei.

The Chondrostei, which have been regarded by some as modified Crossopterygii, are undoubtedly the most generalized of all Teleostomi.

The ventral fins of *Polyodon*, *Acipenser*, and *Scaphirhynchus* have been well described and figured by Thacher * in 1877, and also by Davidoff † in 1879, the former of whom regarded their structure as most important evidence of the truth of his theory of the similar origin of the median and paired fins. This view was also accepted by Bridge ‡, who, in 1878, referring to *Polyodon*, wrote:—"The evident formation of the ventral fins by the coalescence of a series of

* Tr. Connect. Ac. iv. 1877, p. 234, pls. i. & ii.

† Morph. Jahrb. v. 1879, p. 450, pl. xxviii. See also Wiedersheim, 'Gliedmassenskelett,' p. 60 (1892).

‡ Phil. Trans. clxix. 1878, pp. 683–734.

originally distinct cartilaginous rays is clearly indicative of a more primitive condition of these structures than can be found in any other living vertebrate animal."

The Chondrostean ventral fin having been thus described as principally composed of a series of basal cartilages (baseosts) supporting the dermal rays, articulated internally to another series of cartilages (axonosts) which exhibited some fusion anteriorly, it was inexcusably careless of Cope * to propose a classification ignoring this, his order Podopterygia (*i. e.* Chondrostei) being characterized as possessing median fins with numerous axonosts, pectoral *without axonost* and rudimentary baseosts, and ventral with *one axonost* and several baseosts. In Smith Woodward's classification †, which is based on that of Cope, the structure of the paired fins in the Chondrostei has also remained unappreciated. Finally Traquair ‡, in discussing the evolution of fishes, whilst paying considerable attention to the paired fins of Crossopterygii and Dipneusti, does not even think them worthy of notice in the comprehensive order Actinopterygii. So that it would almost seem as if the structure of the paired fins in the Chondrostei, of the highest importance in any discussion as to the affinities of that order and of the very greatest interest as evidence in favour of the lateral fin fold theory, although well known to the morphologists, is in danger of being forgotten by the systematists.

The ventral fins of *Psephurus gladius* are even more primitive than those of *Polyodon* §, and as they have not yet been described, so far as I am aware, I propose to do so and to compare their structure with that of the anal and pectoral fins. All three fins—pectoral, ventral, and anal—strongly resemble each other in external appearance, being extended and composed of numerous articulated dermal rays, at the base of which there is in each case a similar muscular lobe projecting beyond the body-wall, and in which the series of baseosts is imbedded.

On dissection the anal fin is seen to be supported by a series of cartilages, baseosts, 21 in number, which articulate internally with a similar series of axonosts. The latter,

* Am. Nat. xxi. 1887, p. 1017.

† Cat. Foss. Fish. (4 vols. 1889–1901) and Vert. Palæont. (1898).

‡ Presidential Address to Zool. Section of Brit. Assoc. (1900).

§ St. George Mivart, in 1879 (Tr. Z. S. x. p. 457), described and figured the anal fin of *Polyodon* as the ventral, the mistake being due to a wrongly labelled specimen in the Museum of the College of Surgeons, but it is curious to note that on receiving Thacher's paper he did not realize this, but supposed the difference to be due to individual variation.

however, are reduced in number to 18, owing to the fusion of the first 3 and the next 2. The ventral fin is supported by a series of 12 baseosts, exactly similar to those of the anal, which also articulate with a series of axonosts, which in this case are 8 in number, owing to the fusion of the anterior 5. In both anal and ventral the cartilages of the "baseost" series, or radials, show a tendency to segment into 3, thus forming proximal, median, and distal series of segments, whilst external to the last, and completely overlapped by the dermal rays, are a series of short "marginal" cartilages. In the specimen described the anal fin is 23 mm. in length and is composed of 70 dermal rays supported by 21 baseosts, whilst the ventral is 11 mm. in length and is composed of 38 rays supported by 12 baseosts, a proportionate correspondence sufficiently close to be remarkable.

I would submit, then, that the extremely similar structure of the anal and ventral fins in *Psephurus* can only be explained on the theory of a directly similar origin, and that the theory that the structure of the anal is primitive, whilst that of the ventral is derived in some way from a biserial archipterygium, is fantastic and entirely unsupported by evidence. Thus, in an actual living species we have clearer and more complete evidence of the similar origin of the median and paired fins than in the extinct *Cladodus*, which has been considered so important.

The pectoral fin of *Psephurus* is more specialized than the ventral; the baseosts are 7 in number, the anterior 3 being attached to the large coraco-scapular cartilage, which represents the fused anterior axonosts and which underlies a membrane-bone, the cleithrum. The posterior axonosts are also fused to form a single cartilage, the metapterygium. In other living Chondrostei the pectoral fin is very similar to that of *Psephurus*, whilst in the ventral fin the extent of fusion of the axonosts and the number of the baseosts show some variation. In the Palæoniscidæ, so far the earliest and most generalized Chondrostei known, the ventral fins often had an extended * base and were composed of numerous rays. In one genus, the Liassic *Coccolepis*, a series of baseosts have been discovered. The axonosts have not so far been distinguished, but there is every justification for believing that in this generalized family fins so similar to those of *Psephurus* had their supports arranged in the same primitive manner. As regards the pectorals, the coraco-scapular cartilage with

* It is interesting to note that in the Devonian genus *Cheirolepis* the ventral fin is longer than the anal.

the overlying cleithrum must be regarded as typical of the ancestral Teleostome; whether the fusion of the posterior axonosts also is corelated with this, or whether the metapterygium was represented in the early Teleostomi by a series of separate axonosts, there is no evidence to show, but the structure of the pectoral in all Teleostomi is easily explicable as a modification of that of *Psephurus*.

In the structure of their median, as well as of the paired fins, the Chondrostei are essentially primitive, and the condition of the vertebral column also bears witness to their low position. It appears to me fairly well established for both living forms and for those extinct ones which undoubtedly belong to this order that the hyomandibular does not develop a posterior process for articulation with the inner face of the operculum, as is the case in all Teleostei.

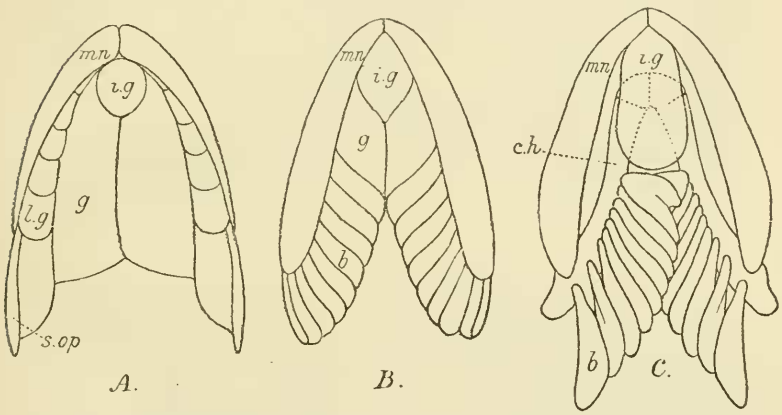

Fig. 1.—Diagrams to show the arrangement of the branchiostegals and gular plates in a typical Crossopterygian, Chondrostean, and Teleost. A. *Rhizodopsis sauroides* (after Traquair); B. *Rhabdolepis macropterus* (after Traquair); C. *Amia calva*. *i.g.*, intergular; *g.*, gular plates; *l.g.*, lateral gulars; *b.*, branchiostegals; *c.h.*, cerato-hyal; *s.op.*, suboperculum; *mn.*, lower jaw.

In the Palæoniscidæ the arrangement of the plates supporting the gill-membranes and extending forward between the mandibular rami, as described by Traquair *, is one from which the conditions which obtain in other Teleostomi are readily derivable. On each side there is a continuous series of obviously homologous plates, the upper two or three of which are enlarged as the opercular bones, those following being the bran-

* Mon. Palæont. Soc., Palæoniscidæ, p. 21 (1877).

chiostegals, the anterior pair of which are considerably larger than the rest and may be termed "gular plates." In front of the gular plates there is sometimes an unpaired "intergular." The anterior branchiostegals and the gular plates occupy the whole of the space between the mandibular rami, to which they are apposed, whilst each meets its fellow in the middle line. Within the order Chondrostei the gular plates and branchiostegals may disappear, but we never get the conditions characteristic of either Crossopterygii or Teleostei.

We have only just begun to realize that the clavicles proper (infraclavicles) which Parker thought he recognized in so many Teleostean fishes (Siluridæ, Hemibranchii, Lophobranchii, *Ostracion*) are entirely wanting in that group, and the presence of this bone as a distinct element in the Chondrostei and Crossopterygii becomes therefore of ordinal value.

The arrangement of the bones of the cranial roof in the Chondrostean Palæoniscidæ is essentially similar to that of the more generalized representatives of the other orders (the Dipneusti excepted). Assuming the interfrontal pineal foramen to be a primitive structure, we may expect to discover a Palæoniscid-like fish possessing this feature, and had such a one existed in the early Silurian it would have been in every way fitted to become the progenitor of the Teleostomi.

Crossopterygii.

The Crossopterygii are modified Chondrostei, from which order the more generalized forms differ but slightly. The lobate pectoral fin has been shown by Dollo * to be an adaptive specialization, and is not to be regarded as of greater importance than the lobate pectoral of some Teleosts (e. g. *Periophthalmus*, Pediculati); it may easily have been derived from the Chondrostean type in the following manner:—

The pectoral fin began to be used at times as a support for the body, and even as an ambulatory limb. This change of function produced a changed orientation in the muscular lobe at the base of the fin, which, originally parallel to the body-wall and attached to it for its whole length, became set at an angle to the body and detached from it posteriorly. As the lobe separated the dermal rays extended round on to its inner side. † The arrangement of the skeletal supports scarcely

* Bull. Soc. Belg. Géol. ix. 1895, p. 79.

† I am by no means satisfied that the pectoral fin of the extinct genera *Tristichopterus* and *Eusthenopteron* is correctly described as unibasal. That of *Tristichopterus*, as originally described and figured by

changed, but the metapterygium became segmented (or this segmentation may be primitive, each segment representing an axonost). From such an asymmetrical fin the symmetrical fins of *Ceratodus* would be derived by an increase in length of the lobe and of the number of axial segments and the development of posterior cartilages for the support of the inner series of dermal rays. The evolution of the ventral fins would be on similar lines.

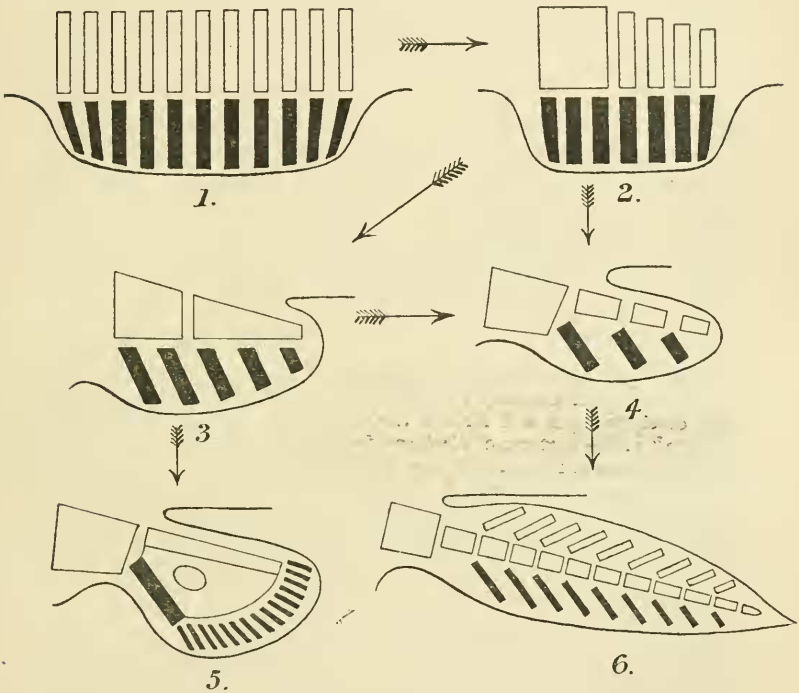

Fig. 2.—Diagrams to illustrate the evolution of lobate paired fins; the axonosts are unshaded, the baseosts shaded. 1, primitive condition; 2 and 3, stages seen respectively in ventral and pectoral of *Acipenser*; 4, obtusely lobate fin; 5, pectoral of *Polypterus*; 6, acutely lobate fin.

In the pectoral fin of *Polypterus* there are two basal pieces articulated to the coraco-scapular ossifications, which

Traquair (Tr. R. Soc. Edin. xxvii. 1876, p. 383, pl. xxxii. fig. 9), would seem to consist of an axis (metapterygium) of three segments and of three baseosts, of which the first appears to be attached to the coraco-scapular.

are inserted close together and diverge distally. Of these the posterior, metapterygium, is the longer, whilst the shorter anterior one is the first baseost. *Polypterus* is peculiar among Crossopterygii in that the metapterygium is not split up into or followed by a series of segments, whilst the baseosts are numerous and are attached to the distal edge of a lamina which has developed between the two basal bones, and in which an ossification has arisen. Nevertheless this type of fin does not appear to me to justify the proposal which has been made to regard the Cladistia as a distinct order.

As to the structure of the ventral fins of the Crossopterygii, in those forms in which they were non-lobate this was probably as in the Chondrostei, and the modern *Polypterus* has an arrangement similar to that which is sometimes seen in *Scaphirhynchus—i. e.*, a single basal piece supporting a short series of baseosts. There is evidence, too, that the supports of the obtusely lobate ventrals were very similar to those of the obtusely lobate pectorals.

The replacement of the branchiostegal rays by the development of the paired gular plates is a characteristic feature of the

---

In *Eusthenopteron* the same arrangement has been described by Whiteaves (Tr. R. Soc. Canada, 1888, p. 87). Before I had seen either of these descriptions I had formed the opinion that the so-called "basal cartilage" in the pectoral of *Eusthenopteron* figured by Smith Woodward (Vert. Palæont. p. 25, fig. 23) was probably coraco-scapular, on account of its shape and bulk, and it appears to me to bear a most suspicious resemblance to the ossification named coraco-scapular by Traquair in *Tristichopterus* and to the coraco-scapular of the recent *Polypterus*. The so-called postaxial process would then be the downwardly projecting portion of the coracoid; otherwise it seems to me to be inexplicable, since the dermal rays do not appear to extend so far, and if such a process developed on the basal segment, why not on the second?

The alternative supposition, which is the one apparently now adopted by Smith Woodward and Traquair (Geol. Mag. 1890, p. 19), is that this bone is the basal segment of the axis. If this be so, then it follows that in the specimens of *Tristichopterus* on which Traquair's description was based this large bone had not been preserved or was hidden.

Unless we assume that *Polypterus* originated independently of other Crossopterygii, it seems to me clear that the primitive Crossopterygian must have had a pectoral in which the first baseost retained its attachment to the coraco-scapular, for I regard the theory that the acutely lobate symmetrical fin has given rise to the obtusely lobate asymmetrical fin as exploded, and I shall require more satisfactory evidence than has yet been forthcoming to convince me that this condition is not realized in *Tristichopterus* or *Eusthenopteron*, as would appear from the original description of each.

I must add that I have been in correspondence with Dr. Traquair, who has very kindly told me that he is not inclined to accept my view, which I put forward here merely for the purpose of stating a case.

Crossopterygii, but the supposed homology of the lateral gulars with the branchiostegals is doubtful. As has been pointed out above, in the Palæoniscidæ the gular plates and branchiostegal rays are serially homologous, whereas the Crossopterygian lateral gulars are plates developed between the principal gulars and the mandibular rami. Moreover, whilst the Palæoniscid branchiostegals are so imbricated that each overlaps the one in front of it, the lateral gulars exhibit precisely the reverse arrangement. Nevertheless, in the Devonian Palæoniscid *Cheirolepis*, as figured by Traquair *, the anterior branchiostegal extends forward between gular plate and lower jaw, and this might be regarded as leading to the Crossopterygian condition.

In the Crossopterygii we see the development of the bone which Boulenger has shown to be the representative of the squamosal of higher Vertebrates. This is fused with the præoperculum in *Polypterus*, but coexists with it in several extinct forms, and corresponds to the upper bone of the postorbital (as distinct from the circumorbital) series of the Palæoniscidæ. The bone internal to it, which is the one usually called squamosal in fishes, is without doubt the true supratemporal †, and should be so named throughout the Teleostomi, whether or no it includes a "pterotic" ossification in certain Teleosts, whilst the series which lie posterior to the parietals and true supratemporals might be termed dermo-occipitals, thus avoiding confusion with the true supraoccipital.

Many Crossopterygii have a pineal foramen, a feature as yet undiscovered in any Chondrostei, and they must have evolved in the Silurian from some primitive type belonging to the latter order.

Dipneusti.

The relations of the Dipneusti to the Crossopterygii have been elucidated by Dollo ‡ in a convincing essay. He gives good reasons for believing that *Dipterus* is the most generalized of all Dipneusti, and that it has originated from a Crossopterygian type closely allied to *Holoptychius*. It is only necessary to add here that his views as to the specialized character of the lobate paired fins receive additional confirmation from the demonstration of the primitive nature of the non-lobate paired fins of the Chondrostei.

* Ann. & Mag. Nat. Hist. (4) xv. 1875, p. 237.

† This conclusion is not invalidated by the fact that *Polypterus* has no supratemporal, the bone so named by Boulenger being the "accessory hyomandibular" of Traquair.

‡ Bull. Soc. Belg. Géol. ix. 1895, p. 79.

Placodermi.

The close relationship of the Coccosteidæ and Asterolepidæ had been generally recognized until they were so widely and unnecessarily separated by Cope, a proceeding which has found more support than it deserved, and I have no hesitation in uniting the groups of which these families are representative, together with the Osteostraci, in a single order of Teleostomi. It has been stated that the bones of the skull of the Coccosteidæ cannot be homologized with those of other Teleostomes; but, as has recently been pointed out by Jækel *, if we take a generalized type such as *Coccosteus*, the

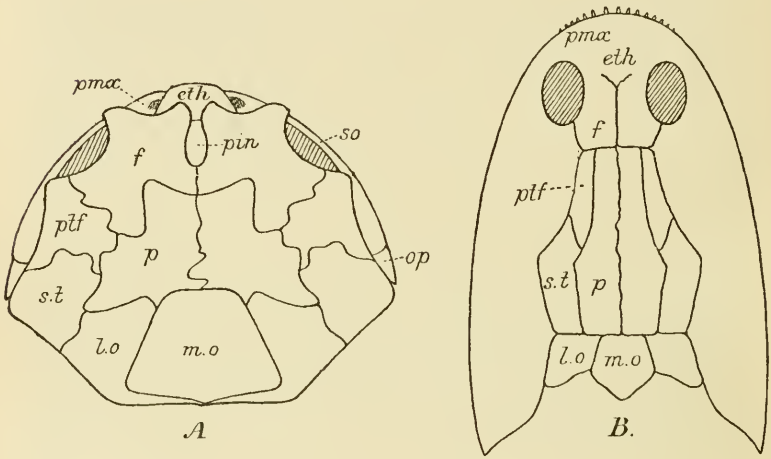

Fig. 3.—Diagrams to show the arrangement of the bones of the cranial roof in *Coccosteus* (A) and in a typical Crossopterygian (*Rhizodopsis*) (B) (both after Traquair). *m.o.*, median dermo-occipital; *l.o.*, lateral dermal occipital; *p.*, parietal; *f.*, frontal; *ptf.*, postfrontal; *s.t.*, supratemporal; *pin.*, pineal; *eth.*, ethmoid; *pmx.*, præmaxillary; *so.*, suborbital; *op.*, operculum.

cranial roof-bones are arranged as in a generalized Crossopterygian or Stegocephalian. Posteriorly we see the three large dermo-occipital plates which we so frequently meet with in the Rhizodontidæ and Osteolepidæ. In front of these are the paired parietals and frontals, the latter bounding the orbits laterally and partly separated medianly by a pineal †

* Sitzb. Ges. naturf. Berlin, 1902, p. 103.

† The pineal plate occupies the position of the pineal foramen of some Osteolepids.

plate. Paired postfrontals and supratemporals are well developed, whilst anteriorly a median ethmoid separates the præmaxillaries. A single large bone on the cheek which sends forward a process below the orbits represents the sub- and postorbitals, and may include the maxillary also. The opercular bones are represented by the operculum only. The nostrils are lateral, between præmaxillary and ethmoid. Gular plates and branchiostegal rays are apparently wanting. In the arrangement of the bones of the cranial roof *Coccosteus* is almost a typical Crossopterygian, and the arrangement of the supports of the dorsal fin in two regular series and the structure of the ventral fin, which appears to be essentially similar to that of *Polypterus* *, cannot be said to negative this view.

A comparison of *Coccosteus* with *Pterichthys* shows the following important points of agreement :—

(1) The anterior part of the trunk is enclosed in an armour of bony plates which are not united to those of the head, so that the latter is freely movable.

(2) There is a single dorsal fin which is membranous.

(3) There is a single opercular bone † and a pitted pineal bone.

(4) *The dermal armour ‡ is in both cases composed of dense bone with a cancellated structure in its thicker portions, with an outer layer of ganoine, with a tuberculated surface, and with open grooves for the sensory canals.*

(5) The arrangement of the bones of the head, but especially that of the dermal plates of the body, can easily be reduced to a common plan.

In the skull of *Pterichthys* we recognize posteriorly the three dermo-occipitals, the supratemporals, and the operculum of *Coccosteus*, whilst anteriorly the median ethmoid and laterally the large suborbital plate are still in the same relative positions. The præmaxillaries are now entirely on the lower surface, but, as in *Coccosteus*, they seem to border the nostrils. The orbits have approached each other until they are only separated by the pineal plate. The postfrontal is fused with the suborbital.

If Jækel be correct in regarding *Homosteus* as intermediate

* It is noteworthy that *Coccosteus* resembles *Polypterus* in the position of the nostrils also.

† In both cases this bone has been interpreted by some authorities as other than opercular, so that it would be perhaps better to say "there is in both a similarly placed bone which may be regarded as an operculum."

‡ See Smith Woodward, 'Vertebrate Palæontology,' p. 12 (1898), and Cat. Foss. Fish. ii. p. xix (1891).

between *Coccosteus* and *Pterichthys*, then the frontals have been displaced forwards and have either disappeared or become fused with the ethmoid or with the suborbital plates, and the so-called postmedian represents the parietals. On the other hand, there is the possibility that this element may be frontal in origin and that the median dermo-occipital may include the parietals, and I incline to this latter view.

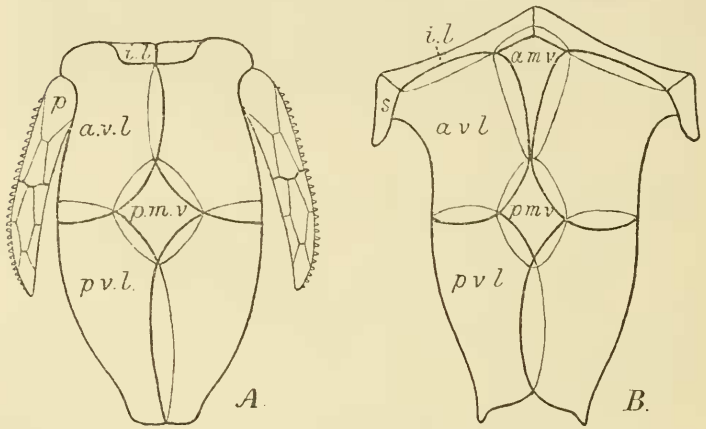

Fig. 4.—Ventral plates of trunk-armour of (A) *Pterichthys* (after Traquair) and (B) *Coccosteus* (after Traquair). *i.l.*, interlateral; *s.*, lateral spine; *p.*, pectoral limb; *a.m.v.*, anterior median ventral; *p.m.v.*, posterior median ventral; *a.v.l.*, anterior ventro-lateral; *p.v.l.*, posterior ventro-lateral. The faint lines indicate the extent of the overlap; the suture between the interlateral and the lateral spine in *Coccosteus* has been inserted.

The arrangement of the plates of the armour of the trunk is on a very similar plan in both Coccosteidæ and Asterolepidæ, 1 or 2 median dorsal plates, 1 or 2 pairs of anterior and posterior lateral plates, and on the ventral surface 4 large plates in exactly the same position and overlapping each other and a smaller four-sided median piece in a very similar manner, whilst a small anterior median plate may or may not be present. The semilunars of the Asterolepidæ seem to correspond to the elements (interlaterals) which have been regarded as clavicles in the Coccosteidæ.

The case of *Acanthaspis* may be cited as evidence of the similarity of the plates of these two families in structure and arrangement. This genus, according to Smith Woodward *,

* Vert. Palæont. p. 16.

"has a dermal armour resembling that of the Antiarcha in minute structure and a ventral plastron quite similar to that of the latter. The lateral appendages, however, instead of being complex and movable, are simple and fixed." Nevertheless Traquair * has given good reasons for regarding *Acanthaspis* as a Coccosteid, and it would even seem that the fixed spinous appendage may be diagnostic of that family.

So far, then, *Coccosteus* has been shown to resemble the more generalized Crossopterygii in the arrangement of the bones of the cranial roof, and reasons have been given for regarding the Asterolepidæ as closely related to the Coccosteidæ †.

What, then, of the peculiar pectoral limb of the Asterolepidæ? It has been sometimes assumed that this is not homologous with the pectoral fin of other fishes, but evidence in support of this assumption has not been forthcoming. Bashford Dean even goes so far as to say that these appendages are now known to be the lateral head-angles [? of *Cephalaspis*] produced and jointed for locomotion. This extraordinary theory is evidently based on a complete misconception as to the position of the Asterolepid limbs, and so needs no discussion. Smith Woodward seems to think that the fixed spinous appendage of *Acanthaspis* in some way supports the view of the independent origin of the Asterolepid pectoral, and I suppose therefore that he regards it as a stage in the development of the latter. Personally, I am unable to imagine that a fixed spine could possibly give rise to a jointed Arthropod-like limb with internal muscles. In fact, the structure of such a limb, articulated to an anterior plate of the body, in which latter is a large foramen, indicating that tendons, blood-vessels, and nerves passed to the muscles of the limb from the body, postulates for me an unarmed ancestor with a muscular limb already developed. Just as the similar limbs of the Crustacea are generally held to have been

* Geol. Mag. (3) x. 1893, p. 148.

† The reasons which have been given for regarding Coccosteids and Asterolepids as not related are (1) the more vascular bone of the latter, (2) the presence of specialized paired fins in the former, and (3) the well-ossified jaws of the Coccosteids. With regard to these, the resemblances in the structure of the bony plates are very remarkable, and the differences are evidently not well marked, or there could be no doubt as to the position of a genus after the minute structure of the bone had been ascertained. The Asterolepid pectoral is surely specialized enough, and it is purely gratuitous to assume its non-homology with that of other fishes.

As to the non-ossified lower jaw of the Asterolepids, instances are not wanting in Chondrostei and Teleostei of degeneration of membrane-bones or of the reversion of a bone to its primitive cartilaginous condition.

derived from the Annelid parapodia, muscular projections used in progression, by increase in size accompanied by hardening and segmentation of the exoskeleton, so do I conceive the Asterolepid limb to have been derived from the lobate Crossopterygian pectoral fin, already being used to support the body and for ambulatory progression, by the development of dermal plates on the muscular lobe of the fin at the same time that the anterior part of the trunk became armoured. The fixed spinous appendage of the Coccosteidæ seems to represent the pectoral limb of the Asterolepidæ, so that we may regard the former as the more generalized in the structure of the skull, the latter in that of the pectoral limb.

We now pass to the Cephalaspidæ and the related forms included in the Osteostraci. The reasons for regarding these as allied to the Asterolepidæ have been given by Smith Woodward, and they appear to me sufficient and convincing, and may be briefly summarized here. In both groups we have a similar caudal region, with a single dorsal fin in the same position and with the caudal fin heterocercal, with a well-developed lower lobe. Then, again, in two Osteostracan genera, *Trematuspis* and *Didymaspis*, the anterior part of the trunk is enclosed in armour, consisting of a dorsal shield to which a ventral shield is opposed, the dorsal shield being distinct from the head-shield in the former genus, but fused with it in the latter. Since the head-shield is continuous, the nostrils must have been inferior, as in the Asterolepidæ, whilst the orbits are approximated and separated only by a pineal plate, as in that family. Finally, the exoskeleton is composed of true bone in its inner layers, as in other "Ganoid" fishes. Where I differ from Dr. Smith Woodward with respect to this group is that whereas he looks upon the genera which most nearly approach the Asterolepidæ as the most specialized, I regard them on that account as the most generalized, and the loose pineal plate and the ganoine layer of *Trematuspis* appear to me in favour of my view. Conceived as specialized and degenerate Asterolepidæ, the structure of the Osteostraci is easily explicable, but I cannot reconcile the Asterolepid structure with the idea that they are a further development of the Osteostraci or of anything like them, whilst if the resemblances between Asterolepidæ and Coccosteidæ are due to convergence (as they must be if they belong to different subclasses), then morphology has ceased to be a guide to relationship. Finally, the Heterostraci must be considered, since they have often been associated with the

Cephalaspidæ, although it has long been known that they differ from them fundamentally in the microscopic structure of their dermal armour, bone lacunæ being entirely absent, whilst there is great similarity to the tooth-structure of the Elasmobranchs. Lankester has strongly maintained that the Heterostraci and Osteostraci are an unnatural association, and as long ago as 1867 he wrote*:—"The Heterostraci are associated at present with the Osteostraci because they are found in the same beds, because they have, like *Cephalaspis*, a large head-shield, and because there is nothing else with which to associate them—the shields are not so closely similar in plan, much less in histological structure†, as to warrant any inference of similarity in other parts." Within the last few years Traquair‡ has discovered new forms which seem to place it beyond doubt that the Heterostraci are armoured Chondropterygii. He has also discovered a new genus, *Ateleaspis*, which he considers is annectent between Heterostraci and Cephalaspidæ, but this view I am not prepared to accept. *Ateleaspis* is certainly very closely allied to *Cephalaspis*, but I cannot see that there is the least reason for regarding it as allied to anything else. The shield is divided superficially into hexagonal areas, which are compared to those of *Cephalaspis*, in which genus this appearance has been shown by Lankester§ to be due to the arrangement of the vascular canals, which may even cause the shield to crack along these lines, whilst in pl. x. fig. 5, a specimen of *Cephalaspis asper* is figured in which the polygonal areas are very strongly brought out by the great pressure and the infiltration to which the shield has been subjected. If Lankester is correct, and the polygonal areas of *Cephalaspis* are due to the arrangement of the vascular canals, then they are not due to the coalescence of originally separate polygonal pieces, as suggested by Traquair, who believes he has found in *Ateleaspis* a stage in this development. Traquair's idea that the superficial tubercles of the shield of *Ateleaspis* represent originally separate Cœlolepid denticles appears to me

* Mon. Palæont. Soc., Cephalaspidæ, p. 62 (1867).

† The difference in structure of the dermal armour of *Pteraspis* and *Cephalaspis* is essentially that between a "placoid" and a "ganoid" scale. There is no reason why the former should not have given rise to the latter and to membrane-bones, by fusion and by the development of a bony substratum, more than once. On the other hand, the evidence shows that the Teleostomi, as here understood, are monophyletic.

‡ Trans. Roy. Soc. Edinburgh, xxxix. 1899, p. 827 *et seq.*, and Rep. Brit. Assoc. 1900, p. 773.

§ 'Cephalaspidæ,' p. 10.

still less valid, and might be applied with equal force to any of the numerous Ganoid fishes with tuberculated bones, and surely it is a retrograde step to suggest that structures which in *Cephalaspis* have been shown to be posterior extensions of the head-shield may after all be pectoral fins.

In fact, the evidence that the Coccosteidæ are Teleostomi, that the Asterolepidæ are allied to the Coccosteidæ, and that the Cephalaspidæ have been derived—through the Trematas-pidæ—from the Asterolepidæ, is so clear, that I am compelled to regard the Ateleaspid structure as a modification of that of the Cephalaspid.

Teleostei.

The reasons for regarding the Teleostei and Chondrostei as distinct orders and for including the Holostei with the former are apparent in the diagnoses given above. The Holostei may then be regarded as the first Teleostean suborder *, distinguished from the Malacopterygii by their well-developed splenial and by one or more of the pectoral baseosts being attached to the metapterygium. Whether certain features of resemblance between *Polypterus* and the Holostei, of which the articulation of the operculum to a posterior process of the hyomandibular is the most important, are to be interpreted as derived from a common ancestor or as due to convergence is not yet clear.

The Palæontological Evidence.

It may be said that the conclusions as to the evolution of the Teleostomi expressed above are not in accordance with the palæontological evidence; but to this I reply that they are in accordance with the morphological evidence, which is clear and sufficiently complete, whilst the geological record is, and must be from the nature of the case, very incomplete. The Teleostomi probably originated from Pleuropterygian Elasmobranchii in the Lower Silurian, and the Crossopterygii, with their specialized offshoots the Dipneusti and Placodermi, must have rapidly evolved, since all are well represented in the Lower Devonian, and the highly specialized Cephalaspidæ are found in the Upper Silurian. In the same way that generalized Reptilia gave rise to the host of forms which

* Provisionally, for I am inclined to think that none of the characters which have been used to distinguish between Holostei and Malacopterygii will prove satisfactory.

were characteristic of the Secondary period, including the highly specialized Ichthyosauria and Pterosauria, which declined and were replaced by a new race, the Mammalia, derived also from the same generalized stock, so must we conceive the primitive Teleostomi as giving rise to the Crossopterygii, with their specialized offshoots the Dipneusti and Placodermi, and remaining dormant to develope later on into the typical Chondrostei. There is no justification for regarding the Crossopterygii as less specialized than the Chondrostei because they were the earlier dominant group. The non-recognition of the true position of *Cephalaspis* as a specialized Asterolepid seems to have been due to its occurrence in the Upper Silurian; but when we consider that, in spite of the imperfect geological record, we know that types so divergent as *Cheirolepis*, *Tristichopterus*, *Holoptychius*, *Dipterus*, *Coccosteus*, *Homosteus*, *Pterichthys*, and *Cephalaspis* were already in being in the Lower Devonian, we may feel assured that some of these, and numerous annectent forms also, must have existed long before.

Summary and Conclusions.

The main results of the foregoing paper may be stated as follows:—

(1) The Chondrostei are the most generalized Teleostomi.
(2) The Crossopterygii differ from them
  (*a*) in the lobate pectoral fin;
  (*b*) in the larger paired gular plates.
(3) The Placodermi (Coccosteidæ, Asterolepidæ, Cephalaspidæ) are a natural group, not related to the Heterostraci, which are Chondropterygii. They may probably be regarded as armoured *primitive* Crossopterygii, this view being most in accordance with
  (*a*) the arrangement of the cranial roof-bones in *Coccosteus*;
  (*b*) the structure of the ventral fin in *Coccosteus*;
  (*c*) the structure of the pectoral limb of the Asterolepidæ.
(4) The Dipneusti probably originated from more specialized Crossopterygii, *e. g.* from the neighbourhood of the Holoptychiidæ.
(5) The Teleostei differ in so many respects from the Chondrostei that they should rank as an order, in which the Holostei are included.

In the Teleostomi and the Chondropterygii * the evolution of the paired fins has proceeded independently, but sometimes on parallel lines, from the earliest stages. The median fins of the Teleostomi also tend to undergo the same modifications as the paired ones, but this comparison must not be pushed too far. The most primitive condition is that which we have seen in the anal and ventral fins of *Psephurus*: (1) dermal rays much more numerous than the baseosts, which form a well-developed series, attached internally to a series of axonosts, the anterior of which show a tendency to fusion. From this stage is easily derived that which is seen in the anal fin of *Eusthenopteron*, or in the ventral of *Polypterus* or ? *Coccosteus*, *i. e.* (2) dermal rays more numerous than the baseosts, which are attached to a single cartilage or bone formed by the fusion of the axonosts. The third stage (3), in which the baseosts are rudimentary or absent and the dermal rays are attached direct to the axonostal bone, is exemplified in the anterior dorsal of the Cœlacanthidæ and the ventrals of the Teleostei.

Two conditions met with in the median fins are not paralleled in the paired ones. The first is a modification of stage (1) described above, and is that seen in the Teleostei, baseosts small or wanting, dermal rays equal in number to the axonosts. The second is derived from stage (2), and is that seen in the posterior dorsal of *Holoptychius*, in which there is a single axonostal cartilage, whilst the baseosts are numerous, crowded, and apparently subdivided, some being attached to others instead of to the axonost.

Similarly the paired fins undergo modifications which

* Thacher (Tr. Conn. Ac. iii. & iv. 1877) deduced the theory of the similar origin of median and paired fins from their similar structure in the Elasmobranchii and Chondrostei. Balfour, from a study of Elasmobranch development, also deduced the similar origin of median and paired fins. He concluded that in modern Elasmobranchii the ventral fin retains in all essential respects its primitive arrangement, and that the pectoral metapterygium represents the pelvic basipterygium. He also wrote: "I should be much more inclined to hold that the fin of *Ceratodus* has been derived from a fin like that of the Elasmobranchii by a series of steps similar to those which Huxley supposes to have led to the establishment of the Elasmobranch fin, but in exactly the reverse direction."

I prefer these conclusions to the more recent ones of Cope and Smith Woodward, who regard the fins of modern Elasmobranchii and Chondrostei as highly specialized, and I would point out that the Ichthyotome pectoral must have been derived from the Pleuropterygian type in the same way as the paired fins of the Dipneusti from those of the Chondrostei, the axis, or metapterygium, representing the series of axonosts, and not being derived from an elongate baseost.

cannot be paralleled in the median ones, when the axonosts form the axis of a lobate fin, and these have already been discussed in treating of the order Crossopterygii.

EXPLANATION OF PLATE VII.

Fig. 1. Anal (A.), ventral (V.), and pectoral (P.) fins of *Psephurus gladius*, the two last from the ventral or inner aspect.

Fig. 2. The same, dissected to show the supporting cartilages. *cor.*, coracoscapular; *mt.*, metapterygium; *a.*, axonosts; *r.*, baseosts (radials); *m.*, marginals.

XL.—*Rhynchotal Notes.*—XXIII. By W. L. Distant.

Heteroptera from the Transvaal.

The British Museum has secured a set of the specimens of Rhynchota collected by the Rev. H. A. Junod at Shilouvane, Zoutpansberg, Northern Transvaal, and this paper refers to undescribed species found in the collection. The Capsidæ have already been described (*ante*, p. 196 *et seq.*), while the Homoptera, poorly represented, are reserved for future treatment. The greater part of the Zoutpansberg district possesses a subtropical climate and is much covered with bush and dwarf forest, thus being in strong contrast with the high and barren veld which constitutes so large a portion of the Transvaal landscape. I was therefore not greatly surprised to find both many new species and others known in entomological record, which I had neither seen nor secured during four years' collecting in other parts of the Transvaal. Two genera, *Geomorpha* and *Phonolibes*, both hitherto represented only by a single West-African species, are now found to have each a representative species in North Transvaal.

All the types are contained in the National Collection.

Fam. Pentatomidæ.

Subfam. *Cydninæ*.

Gnathoconus elongatus, sp. n.

Elongate; black; lateral margins of pronotum, basal half of lateral margins of corium, second and base of third joints of antennæ, tibiæ (excluding apical third), lateral margins of the fourth, fifth, and sixth abdominal segments, and the apical